How wild wolves became domestic dogs

Research sheds new light on the origin of humanity's most intimate quadruped ally

"The poor dog," wrote poet Lord Byron in a flight of emotion, "in life the firmest friend, The first to welcome, foremost to defend." And certainly, few animal lovers would care to differ. The dog, after all, is commonly referred to as man's best friend, and unquestionably serves a wide range of human purposes. Thanks to artificial selection, there are dogs that guard houses and dogs that herd livestock, dogs that locate game birds for shooting and dogs that retrieve game birds that have been shot, dogs that pull sleds and dogs that sit languidly in human laps.

Clearly, the relationship between dog and human runs deep in our culture and our psyches. No surprise, then, that the origin of the domestic dog has long been a matter for speculation and inquiry. But now, new techniques of molecular biology are allowing researchers to trace dog ancestry and to compare species and even breeds in ways previously unavailable to traditional wildlife biologists, taxonomists, and archeologists. Investigators are making great strides in understanding the origin of the domestic dog, even though results are often subject to dispute and controversy, as might be expected of research on a creature that is genetically complex.

"No other species is so diverse," says Robert Wayne, a University of California–Los Angeles evolutionary biologist who has just completed the largest study ever on dog genetics and evolution. "Dogs are a model for how rapid morphological change might take place in a natural population." They also offer clues as to how genetic vigor can be maintained in domestic species.

One of the key questions of dog evolution focuses on the source: From what wild creature did the domestic dog arise? Charles Darwin suggested that the close relationship between wolves, coyotes, and jackals—all of which can interbreed—so muddies questions of which species yielded the dog that "we shall probably never be able to ascertain [the dog's] origins with certainty." Austrian behaviorist Konrad Lorenz added fuel to the fire in the 1950s by suggesting that some dog breeds may derive from jackals, others from wolves. Other biologists have proposed that dogs sprang from coyotes. Archeological evidence collected at ancient human homesites does not help, because the bones of animals in the process of domestication generally do not reveal intermediate steps between wild forebears and modern domestic animals.

New genetic evidence marshaled by Wayne and his colleagues lends strong support to the wolf advocates. As Wayne's team reported in the 13 June *Science*, they analyzed mitochondrial DNA from 140 domestic dogs representing 67 breeds and five crossbreeds, then compared the dogs' sequences with DNA from 162 wolves collected at 27 localities worldwide as well as with DNA from five coyotes and eight Simien, two golden, and two black-backed jackals.

"The genetic data strongly suggest that the wolf is the progenitor of the domestic dog," Wayne says. Dog gene sequences differ from those of wolves by at most 12 nucleotide substitutions, whereas dog sequences differ from coyote and jackal sequences by at least 20 substitutions and two insertions. Coyotes and jackals are thus "very different [genetically] from wolves and dogs," Wayne says.

Identifying these genetic differences did more than establish the wolf as ancestor to the domestic dog. It also yielded further conclusions about dog evolution that surprised even Wayne himself and engendered dispute with other experts.

Based on studies of canid bones found at human archeological sites, researchers have traditionally placed the domestic dog's origins at about 10,000–14,000 years ago. As discussed in the *Science* article, Wayne and his colleagues' molecular data indicate that the dog actually is much older. Wayne's lab did a smaller study of wolf and dog nuclear DNA which showed that the two animals differ by only 1–2% of their gene sequences. Because fossil data show that wolves and coyotes, which differ genetically by 7.5%, diverged approximately 1 million years ago, Wayne calculates that the genetic difference between

by Jeffrey Cohn

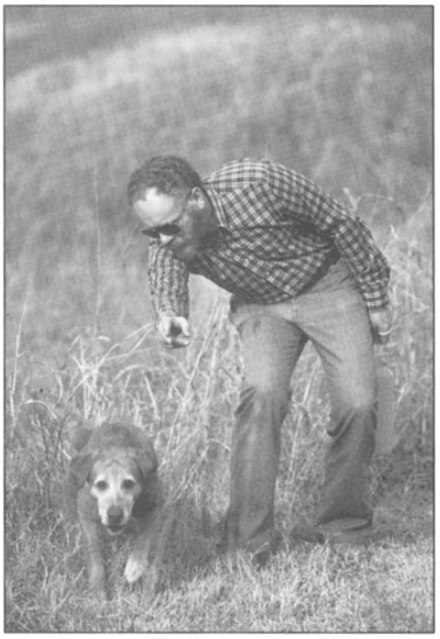
wolf and dog suggests that they separated about 135,000 years ago. If his conclusion is correct, then the dog is by far humanity's oldest domestic animal. The second oldest is the domestic pig, which archeologists believe originated 10,000 years ago.

Such a surprising assertion has inevitably spawned controversy. If wolves and dogs diverged when Wayne suggests, some experts ask, then why does the archeological record fail to show morphological differences between wolf and dog fossils until about 14,000 years ago? Wayne guesses that a phenotypic divergence between the two animals began only after humanity converted from hunter–gatherer cultures to more agricultural societies about 10,000–15,000 years ago, imposing new selective regimes on dogs.

Darcy Morey, an adjunct assistant professor at the University of Tennessee–Knoxville whose doctoral dissertation focused on the evolution of humankind's relationship with the dog, disagrees with Wayne's interpretation of the evidence. "How could so fundamental an ecological change occur between wild and domestic populations without altering the animals' size and form?" Morey asks.

Wayne's research is "an elegant study," geneticist Stephen O'Brien says, but it presumes that the mitochondrial DNA clock runs at a constant rate through time. "That might not be correct," says O'Brien, chief of the National Cancer Institute's Laboratory of Genomic Diversity in Frederick, Maryland. O'Brien, who has done genetic studies on wild and domestic cats, says that calculating precise dates is difficult, particularly if altered sex ratios or population bottlenecks affect a species' evolution.

Wayne agrees that mitochondrial DNA, which evolves rapidly and at uneven rates of change, gives only a rough estimate of the evolutionary relationship between species. But, because mitochondrial DNA does mutate rapidly, he believes that it is the best currently available method for gauging genetic change. He admits that his study may inflate the date of origin for the domestic dog, but he contends that his evidence is nevertheless correct in indicating that the dog did arise long before the date ascribed to it by archeological evidence. Wayne plans to test microsatellites, a set of fast-evolving nuclear genes, to confirm the mitochondrial DNA results.



A hunter trains his laborador retriever by throwing decoys that the dog is ordered to return. By modifying through artificial selection the innate behavior of the dog's wolf ancestor, such as the urge to chase prey, humankind has produced a domestic animal of many abilities. Photo: Oklahoma Department of Wildlife Conservation.

Wolves become dogs

Regardless of when wolves came into the human domain, the relationship wrought fundamental changes on the wolf, remolding the wild animal. Most notably, dog skulls, teeth, and brains are smaller than those of wolves. An adult dog with the same head size as an adult wolf has a 20% smaller brain, says Ray Coppinger, a professor of biology at Hampshire College in Amherst, Massachusetts, who has spent years studying dog evolution and behavior. And an adult dog of the same weight as an adult wolf has a 20% smaller head. Also, some physical traits that do not appear in wolves are common in dogs, including a sickle-shaped tail, floppy ears, and piebald color patterns.

Dogs and wolves differ in their behavior as well. For example, female dogs usually come into heat twice yearly, but wolves only once. Moreover, many adult dogs beg for food, a behavior typical of wolf puppies but not of adults. Dogs greet and lick their human masters the way wolf pups do their elders.

Some of the physical traits characteristic of certain dog breeds, such as floppy ears and rounded profiles, do appear in wolves, but only as pups. This appearance of youthful wolf traits in adult domestic dogs suggests that dogs are neotenic, forever immature.

Morey suggests that retention of juvenile morphological and behavioral traits by adult dogs was due to natural, rather than artificial, selection. Presumably, dog domestication began when humans captured wolf pups and raised them as pets. In the wild, mature wolves leave the natal pack to seek mates and start their own packs, or they challenge the dominant animals in their packs and take over. Animals that did this to human masters would likely be killed, giving them little opportunity to contribute to the gene pool of the domestic dog.

The wolves that survived in the human environment and gave rise to dogs probably were individuals that preserved into adulthood the submission that wolf pups demonstrate toward adult wolves. This selection for submission presumably led to other puppylike behavioral traits continuing into maturity among the animals that successfully adapted to life in the shadow of humankind. "The consistent appearance of these traits in dogs living within so many different [human] cultures suggests

that selection pressures broader than cultural ones brought about the changes," Morey says.

Coppinger suspects that the genetic changes that allowed behavioral adaptation to the human environment led as well to the morphological changes characteristic of dogs, because some physical and behavioral changes may be genetically linked. Wayne agrees. "A lot of characters are linked genetically," he says. "One change can affect various characteristics. Some things, like skull length, are controlled by many genes. If you change one gene or group of genes, that can affect several characteristics." Whether the theory holds true for dog behavior and morphology remains to be proved, Wayne adds.

One experiment conducted in Russia in the 1960s and 1970s supports Coppinger's ideas about a link between morphological and behavioral changes. D. K. Belyaev deliberately bred silver foxes, a subspecies of the red fox, for tameness. Belyaev, then of the USSR Institute of Cytology and Genetics, was seeking to develop animals suitable for fur ranching.

Belyaev observed that female silver foxes that were less aggressive than average and that lacked a fear of humans—necessary traits for tameness—also came into estrus and bore young independent of seasons. "The reorganization of the genetic basis of reproduction...might have evolved through selection for certain behavioral responses, which may be especially characteristic of the early stages of domestication," Belyaev wrote in the journal *Genetics and Physiology* in 1977.

More telling still in terms of a genetic linkage between behavioral and morphological traits is the fact that, during 20 generations of selective breeding for tameness, Belyaev's foxes developed morphological traits familiar among domestic dogs but not found in wild canids: hooked tails, drooping ears, twice-a-year breeding, and, in some cases, black-and-white piebald coats.

The question of where

The subject of dog evolution is rich with unanswered questions, a garden of inquiry for the evolutionary biologist. In addition to determining which wild species yielded the domestic dog and when, Wayne, when setting out on his genetic studies, had hoped that his research would help to locate the area of the globe in which dogs first appeared. But when he tried to link dog gene sequences to those of living wolf populations, he failed. He could not even determine whether dogs sprang from wolves once or several times.

One expert contends that no single point of origin exists. Stanley Olsen, a retired anthropologist at the University of Arizona in Tucson and author of the 1985 book *Origins of the Domestic Dog*, says that fossil evidence from hundreds of human archeological sites in Europe, the Near East, and Asia suggests that dogs evolved from different wolf populations in different places at different times. Olsen believes that large dogs may have derived from the large wolves of northern Europe, whereas small ones came from Asian and Near Eastern wolves.

Yet another study further complicates the issue by proposing three separate dog lineages. Ben Koop, a biologist at the University of Victoria in British Columbia, has been researching the genetics of extinct Native American dogs from the Canadian northwest. The ancestors of these animals crossed the dry Bering Strait with humans during the most recent Ice Age.

Using phylogenetic analysis on museum specimens of these Native American dogs, Koop compared the specimens' mitochondrial gene sequences with those of museum-specimen and living wolves, coyotes, and foxes and of living domestic dogs. He found that gene sequences from the Native American dogs grouped together. The Native American dogs were more closely related to wolves than to domestic dogs, possibly because wolves and Native American dogs interbred occasionally.

Similarly, Koop found that all domestic dog breeds form a single group distinct from that of Native American dogs. That suggests, he says, that domestic dogs have a single, rather than multiple, origin, but arose apart from Native American dogs. But Koop also found an exception—the Arctic elkhound apparently evolved separately from all other dog breeds. It is the only breed known to have done so.

Koop's research, by suggesting three dog lineages, so complicates theories about dog origin that Koop himself, looking over his data, says, "I'm confused. It's new data that provides a new perspective, but it clouds the issue. You have to remember we have preliminary results based on what DNA we can get out of old museum hides. The material we had was pretty beat up."

Wayne's studies suggest that the dog's complicated evolutionary history has yielded an animal of great genetic diversity. Even recognized dog breeds show remarkable genetic variation. Part of this diversity, Wayne thinks, stems from intermittent breeding that occurred between dogs and wolves even after domestication, providing raw material for

artificial selection under human control and giving the dog great evolutionary plasticity.

The role that backcrossing with wolves played in the dog's genetic vigor may serve as a model for artificial selection, Wayne's work suggests. Domestic plants and animals whose feral forebears are now extinct cannot avail themselves of genetic enrichment from wild populations, presumably putting a limit on how much they can be modified by artificial selection in the future. "Consequently," Wayne and his colleagues conclude in their *Science* article, "the preservation of wild progenitors may be a critical issue in the continued evolution of domestic plants and animals." ❑

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